Host Ranges of Six Solitary Filth Fly Parasitoids (Hymenoptera: Pteromalidae, Chalcididae) from Florida, Eurasia, Morocco, and Brazil

CHRISTOPHER J. GEDEN,[1] ROGER D. MOON,[2] AND JERRY F. BUTLER[3]

USDA–ARS, Center for Medical, Agricultural and Veterinary Entomology, PO Box 14565, Gainesville, FL 32607

Environ. Entomol. 35(2): 405–412 (2006)

ABSTRACT Attack rates, progeny production, sex ratios, and host use efficiency of *Muscidufurax raptor* Girualt and Sanders, *Spalangia cameroni* Perkins, *S. endius* (Walker), *S. nigroaenea* Curtis, *S. gemina* Boucek (Hymenoptera: Pteromalidae), and *Dirhinus himalayanus* (Hymenoptera: Chalcididae) were evaluated in laboratory bioassays with five dipteran hosts: house fly (*Musca domestica* L.), stable fly (*Stomoxys calcitrans* L.), horn fly (*Hematobia irritans* L.), black dump fly [*Hydrotaea aenescens* (Weidemann)] (Diptera: Muscidae), and a flesh fly (*Sarcophaga bullata* Parker) (Diptera: Sarcophagidae). *M. raptor*, *S.cameroni*, and *S. endius* readily attacked and produced progeny on all five host species, with substantially lower production from *S. bullata* than from the muscid hosts. Rates of host attacks by *S. nigroaenea* and *S. gemina* were similar on house fly, stable fly, and black dump fly hosts, with lower rates on horn fly; almost no progeny were produced by *S. nigroaenea* on *S. bullata* hosts. *D. himalayanus*, a large-bodied chalcidid parasitoid, had highest rates of host attacks and progeny production on *S. bullata* and *H. aenescens*, followed by stable fly and house fly hosts; very few progeny were produced by this species on horn fly hosts. Overall differences among different geographic strains of parasitoids (from Russia, Kazkhstan, and Florida) were generally small, although the Florida strain of *M. raptor* was superior to the two Eurasian strains.

KEY WORDS Muscidifurax raptor, Spalangia cameroni, Spalangia endius, Spalangia nigroaenea, Dirhinus himalayanus

PUPAL PARASITOIDS ARE AMONG the most important and common natural enemies of filth flies associated with animals and humans (Rutz and Patterson 1990). Augmentative releases of parasitoids can increase parasitism levels in the field, sometimes to an extent sufficient to provide satisfactory suppression of fly populations (Morgan and Patterson 1990, Geden et al. 1992a, Petersen and Cawthra 1995, Crespo et al. 1998, 2002, Skovgard and Nachman 2004). In other instances, parasitoid releases have had little impact on fly populations or parasitism levels (Meyer et al. 1990, Andress and Campbell 1994, Weinzierl and Jones 1998, McKay and Galloway 1999, Kaufman et al. 2001). Although the factors that determine success of augmentative releases are unclear and may be site-specific, failures may have been caused by sensitivity of parasitoids to pesticides, unfavorable manure conditions, disease problems in parasitoid cultures, and an imperfect understanding of how to match candidate parasitoid species with target pests and breeding conditions (Rutz and Axtell 1981, Petersen et al. 1983, Morgan and Patterson 1990, Geden et al. 1992b, 1995).

A better understanding of niche characteristics of parasitoid species could assist in the process of matching parasitoid species with release sites. Different parasitoid species have been evaluated in recent years with regard to temperature-dependent attack rates, development time, manure moisture preferences, and the effect of habitat type and depth on foraging behavior (Geden 1996, 1997, 1999, 2002). Host range is another niche characteristic that may vary among species of fly parasitoids. Most of the available literature on muscoid fly parasitoids has involved trials with house flies (*Musca domestica* L.) and stable flies (*Stomoxys calcitrans* L.). By comparison, information on parasitism of other species such as the horn fly (*Hematobia irritans* L.) is limited and mostly deals with field surveys of flies in various locations (McKenzie and Richerson 1993, Mendes and Linhares 1999, Sereno 2000, Marchiori et al. 2000, 2002).

In 1999, one of us (R.D.M.) collected fly parasitoids from cattle farms in Russia and Kazakhstan. From these collections, we established colonies of Russian and Kazakhstan strains of *Muscidifurax raptor* Girault and Sanders, *Spalangia endius* (Walker), *S. cameroni* Perkins, and *S. nigroaenea* Curtis, thus providing an

[1] Corresponding author, e-mail: cgeden@gainesville.usda.ufl.edu.
[2] Department of Entomology, Hodson Hall, University of Minnesota, St. Paul, MN 55108.
[3] Department of Entomology and Nematology, University of Florida, Gainesville, FL 32611.

Table 1. Sources of *M. raptor*, *S. cameroni*, *S. endius*, *S. nigroaenea*, *S. gemina*, and *D. himalayanus* used in host range bioassays

Species	Origin	Year of collection	Type of farm	Host(s) at time of collection
M. raptor	Florida	1992	Poultry	House fly
M. raptor	Russia	1999	Dairy	House fly, stable fly
M. raptor	Kazakhstan	1999	Dairy	House fly, stable fly
S. cameroni	Florida	1999	Dairy	House fly
S. cameroni	Russia	1999	Dairy	House fly, stable fly
S. cameroni	Kazakhstan	1999	Dairy	House fly, stable fly
S. endius	Florida	1998	Dairy	House fly
S. endius	Russia	1999	Dairy	House fly, stable fly
S. endius	Kazakhstan	1999	Dairy	House fly, stable fly
S. nigroaenea	Russia	1999	Dairy	House fly, stable fly
S. nigroaenea	Kazakhstan	1999	Dairy	House fly, stable fly
S. gemina	Brazil	1991	Poultry	House fly
D. himalayanus	Morocco	1991	Unknown	House fly

opportunity to evaluate potential differences among strains for performance on different fly hosts. The objectives of this study were to (1) evaluate potential differences among geographic strains of these species and (2) examine performance of these and two other solitary parasitoids on a range of host species.

Materials and Methods

Parasitoid Colonies. Three colonies of *M. raptor* were tested; one was originally collected from a poultry farm in Brooksville, FL, in 1994; the other two were from dairy farms near Kraznodar, Russia, and Almaty, Kazakhstan, in 1999 (Table 1). Three colonies of *S. cameroni* were tested from dairy farms in Bell, FL, in 1998 and near Almaty and Kraznodar in 1999. Three colonies of *S. endius* were tested: one from Florida poultry farms in 1998 and the others from dairy farms near Almaty and Krasnodar in 1999. Two colonies of *S. nigroaenea* were tested from dairy farms near Almaty and Kraznodar in 1999. Single colonies of *D. himalayanus* and *S. gemina* were collected from farms in Morocco (1991) and Brazil (1992), respectively. Colonies were maintained by providing parasitoids with 2-d-old house fly pupae three times per week at a host:parasitoid ratio of ≈10:1 in chambers maintained at 25°C, 60–80% RH under constant darkness.

Fly Colonies. House flies and stable flies were from long-established colonies maintained at CMAVE and were reared using standard methods and diets (Hogsette 1992). Black dump flies, *H. aenescens*, were from a colony established from Florida poultry farms in 1989 and reared using the methods described in Hogsette and Washington (1995). Two-day-old pupae were separated from rearing media by water flotation and dried in a forced air blower designed for this purpose (Bailey 1970).

Horn flies were from a colony originally established in the 1970s by J.F.B. Adults were reared in cages at 26°C, 60–80% RH, and constant light and given bovine blood daily by placing blood-soaked pads on the tops of the cages. Blood for the colony was collected every 2 wk at a local abattoir in 8.5-liter batches and treated with 30 g of sodium citrate, 1.5 g of kanamycin sulfate, and 250,000 U of nystatin. Eggs were collected daily on water-soaked cotton pads placed 1 cm below the screened cage bottoms. Larvae were reared by placing 1 ml of eggs on a rearing medium composed of 1 liter of steer manure, 1 liter of pelletized peanut hulls soaked overnight in 750 ml water, and 115 g of a prepared mixture of wheat flour (44%), fish meal (33%), alfalfa meal (18%), and baking soda (5%). Larval trays were kept in the same room as the adult flies, and pupation occurred on day 5 under these rearing conditions. Pupae were separated from media by water flotation and dried in a forced-air blower 7 d after egg placement.

The flesh fly, *S. bullata* Parker, was originally obtained from Carolina Biological Supply Co. (Burlington, NC). Adult flies were given water and moist sugar-yeast cakes. The cakes were prepared by mixing three parts sugar and one part yeast hydolyzate (by volume) and holding the mixture in pans at 90% RH for 3 d. Flies were presented with fresh beef liver for larviposition. Larvae were reared on beef liver and pupated ≈7 d after larviposition on paper towels or vermiculite placed under larval rearing pans.

Samples of 100 pupae of each species were weighed for each cohort used in the bioassays and averaged as follows: 106 mg (*S. bullata*), 18 mg (house fly), 15 mg (stable fly and *H. aenescens*), and 5.5 mg (horn fly).

Bioassay Procedure. Tests were conducted by exposing groups of 100 fly pupae of a given species to five female parasitoids (3–5 d old) in 30-cm^3 cups with screen-topped lids for either 24 (*M. raptor*) or 48 h (all other species). Fly pupae in the tests were ≈48 h old except in those with *S. bullata.* Because of the long duration of the pupal stage in this species (10–12 d under our conditions), pupae of *S. bullata* were tested when they were 4 d old. For each test date and host species, sets of 100 pupae with no parasitoids were set up and handled in the same manner. After exposure to parasitoids, pupae were removed and held for fly and parasitoid emergence. Uneclosed pupae and parasitoids were counted and sexed (except for *D. himalayanus*) after parasitoid emergence ceased. Sex determination was not done with *D. himalayanus* because of the difficulty of distinguishing males from females in dried specimens. We also calculated the proportion of killed pupae from which parasitoid progeny emerged. This value, termed "host use" here,

Table 2. Mean (SE) no. host attacks and progeny produced by three strains of *M. raptor* using five species of hosts

Host	No. hosts killed	No. progeny produced	Percent females	Host use
Russian strain				
Horn fly	42.8 (3.5)b	30.2 (3.0)ab	57.2 (2.4)a	68.4 (4.4)a
House fly	52.0 (4.1)b	42.0 (4.2)a	63.4 (2.6)a	79.2 (3.8)a
Stable fly	68.7 (4.0)a	53.1 (3.3)a	51.9 (3.3)a	78.0 (3.7)a
S. bullata	30.1 (4.4)b	16.7 (3.9)b	53.8 (6.2)a	43.6 (8.5)b
H. aenescens	72.0 (3.1)a	51.3 (2.0)a	55.3 (3.0)a	71.8 (1.9)a
ANOVA *F*	20.33[a]	20.43[a]	1.65[a]	8.18[a]
Kazakhstan strain				
Horn fly	42.5 (3.7)b	32.4 (3.1)b	57.1(2.4)ab	75.9 (2.7)a
House fly	64.5 (5.0)a	51.8 (3.8)a	65.0 (3.0)a	90.9 (2.4)a
Stable fly	65.1 (4.5)a	46.8 (3.5)a	53.0 (4.0)ab	73.1 (4.0)a
S. bullata	34.7 (5.8)b	21.4 (5.1)c	68.5 (4.7)a	46.4 (8.0)b
H. aenescens	61.5 (4.4)a	39.7 (3.4)b	50.6 (5.6)b	73.1 (4.1)a
ANOVA *F*	9.07[a]	9.65[a]	3.49[b]	9.78[a]
Florida strain				
Horn fly	66.7 (4.5)a	54.7 (3.7)a	48.6 (4.0)a	82.3 (1.4)a
House fly	77.1 (3.4)a	62.7 (3.5)a	51.3 (7.2)a	81.3 (2.9)a
Stable fly	83.3 (4.0)a	69.4 (4.1)a	53.0 (3.0)a	82.8 (1.9)a
S. bullata	42.9 (5.5)b	23.5 (4.6)b	39.7 (9.6)a	44.9 (7.8)b
H. aenescens	65.5 (4.6)a	48.5 (3.5)ab	40.6 (4.8)a	74.0 (1.7)a
ANOVA *F*	11.62[a]	19.88[a]	1.05[c]	17.75[a]

$n = 15$ sets of five females (five separate tests of three sets each) with 100 host pupae of each species for a 24-h exposure. Host use is the percent of killed hosts from which adult parasitoids emerged. Means within columns of the same strain followed by the same letter are not significantly different at $P = 0.05$ (Tukey's HSD). ANOVA df = 4,70.

[a] $P \leq 0.01$; [b] $P \leq 0.05$; [c] $P > 0.05$.

would be 1.0 if every killed host produced a parasitoid. Actual values reflect the efficiency with which the parasitoids use available hosts, host-feeding events without oviposition, host rejection after stinging, and mortality of parasitoid immatures. Three sets of pupae and parasitoids were tested on each of five separate occasions, for a total of 15 observations for each host species and parasitoid combination. Host mortality among controls was used for quality control, and tests were rejected and repeated if control mortality exceeded 10%.

Data Analysis. Separate one-way analyses of variance (ANOVAs) were performed for each parasitoid colony to evaluate the effect of host species on the number of host pupae killed, the number of parasitoid progeny produced, the proportion of females among progeny, and host use as defined in the previous section. In addition, the effects of host species, parasitoid strain, and host × strain interaction were examined by two-way ANOVA for those species in which more than one strain was tested (*M. raptor*, *S. nigroaenea*, *S. cameroni*, and *S. endius*). Data representing proportions (sex ratio and host use) were subjected to arcsine transformation before analysis and are presented as percentages in the tables. Data were analyzed using the GLM procedure of the Statistical Analysis System (SAS Institute 1992).

Results

Muscidifruax raptor attacked and produced progeny from all five species of hosts (Table 2), although fewer *S. bullata* were attacked and fewer progeny produced (16.7–23.5) from this host than the other species. Differences in progeny production from the other host species ranged from 30.2 progeny produced (Russian strain with horn fly) to 69.4 (Florida strain with stable fly). Differences in sex ratios were small and only significant for the Kazakhstan strain, where *M. raptor* produced relatively lower proportions of females on *H. aenescens* (50.6%) than on house fly (65%) and *S. bullata* (68.5%). Host use was significantly lower with *S. bullata* hosts (43.6–46.4% of killed hosts produced progeny) than with the other species, ranging from 68.4 (Russian strain with horn fly) to 90.9% (Kazakhstan strain with house fly). Overall strain differences were significant, with the Florida strain having higher overall rates of host attack and progeny production and lower proportion females than the two Eurasian strains (Table 3).

The Florida strain of *S. cameroni* killed similar numbers of host pupae of all five species (67.1–72.9), although progeny production and host use were lower on *S. bullata* than other host species (Table 4). The Russian and Kazakhstan strains had lowest rates of host attack (36.9 and 47.5 killed pupae, respectively) and progeny production (17.7 and 25.8 progeny produced) on *S. bullata;* differences among the other species were small, although both Eurasian strains had the highest rates of host attack (76.0 and 89.3 killed pupae, respectively) and progeny production (56.3 and 67.7 progeny produced) on *H. aenescens.* Sex ratio differences were small; however, proportionally fewer females emerged from *H. aenescens* than the other fly species in the Russian (17.1% females) and Florida strains (16%). Host use by *S. cameroni* was lower on *S. bullata* than the other four species. There were no significant overall strain differences with respect to progeny production, sex ratios, or host use (Table 3). Attack rates of *S. cameroni* were significantly affected by host and the host × strain interaction.

Table 3. ANOVA *F* values for effects of parasitoid strain and host species on host attacks and progeny production of *M. raptor*, *S. nigroaenea*, *S. cameroni*, and *S. endius*

Species	No. hosts killed			No. progeny produced			Percent females			Host usea		
	Strain	Host	Host × strain	Strain	Host	Host × strain	Strain	Host	Host × strain	Strain	Host	Host × strain
M. raptor[b]	17.6[e]	33.4[e]	2.6[f]	22.8[d]	42.4[d]	3.4[d]	9.3[d]	2.3[f]	1.5[f]	2.1[f]	31.6[d]	0.9[f]
S. cameroni[b]	8.1[d]	18.9[d]	4.1[d]	2.4[f]	41.8[d]	3.7[d]	0.7[f]	4.1[d]	2.3[e]	1.7[f]	35.4[d]	3.9[d]
S. endius[b]	3.6[e]	57.7[d]	1.0[f]	7.5[d]	79.9[d]	0.6[f]	0.1[f]	1.6[f]	0.7[f]	1.5[f]	22.9[d]	0.6[f]
S. nigroaenea[c]	0.4ns	42.3[d]	0.6[f]	1.0[f]	34.9[d]	0.5[f]	9.7[d]	2.5[e]	0.8[f]	2.8[f]	33.0[d]	0.8[f]

Host species tested were horn fly, house fly, stable fly, *S. bullata*, and *H. aenescens*.
[a] Percent of killed hosts from which adult parasitoids emerged.
[b] df = 2 (strain), 4 (host), 8 (interaction), and 210 (error).
[c] df = 1 (strain), 4 (host), 4 (interaction), and 141 (error).
[d] $P \leq 0.01$; [e] $P \leq 0.05$; [f] $P > 0.05$.

All three strains of *S. endius* attacked significantly fewer *S. bullata* (41.3–50.7 pupae killed) and produced fewer progeny on this host (23.4–24.5 parasitoid progeny) than on the other four fly species, followed by horn fly (Table 5). Rates of host attack and progeny production by the three *S. endius* strains were similar on house fly (81.6–85.1 pupae killed, 57.8–65.3 progeny produced), stable fly (73.9–88.2 pupae killed, 48.2–60.4 progeny produced), and *H. aenescens* hosts (82.1–94.5 pupae killed, 60.9–73.3 progeny produced); the only significant difference observed among the hosts was with the Russian strain, which attacked and produced progeny from significantly more house fly hosts than those of the stable fly or *H. aenescens*. Sex ratios were unaffected by host species (overall range, 59.9–71.7% females). Host use was lowest for *S. bullata* (48–57% successful parasitism) and similar among the other four species of hosts (overall range, 66.3–78.8%). Parasitoid strain had a significant effect on host attacks and progeny production by *S. endius*, reflecting an overall trend of higher rates of both traits in the Russian and Florida strains of this species (Table 3). Parasitoid strain had no significant effect on host use.

Both the Russian and Kazakhstan strains of *S. nigroaenea* attacked significantly fewer *S. bullata* (15.1 and 10.8 pupae killed, respectively) than the other four hosts and produced very few progeny on this species (3.5 and 1.9 progeny produced, respectively; Table 6). The highest rates of host attack and progeny production were on house fly and *H. aenescens* (61.2–66.4 pupae killed, 26.6–38.9 progeny produced). Sex ratio was unaffected by host species (overall, 41.3–66.3% females). Host use by *S. nigroaenea* was much lower with *S. bullata* (17.2 and 8.3% successful parasitism by the Russian and Kazakhstan strains, respectively), than with the other four fly hosts (overall, 42.4–59.1% successful parasitism). Parasitoid strain had no significant effect on attack rates, progeny production, or host use (Table 3); however, the Kazakhstan strain produced a significantly higher proportion of females overall (51.9–66.3%) than the Russian strain (41.3–55.9%).

Table 4. Mean (SE) no. host attacks and progeny produced by three strains of *S. cameroni* using five species of hosts

Host	No. hosts killed	No. progeny produced	Percent females	Host use
Russian strain				
Horn fly	65.3 (3.2)a	51.0 (2.2)a	38.6 (5.5)ab	78.7 (1.7)a
House fly	61.6 (3.6)a	49.8 (3.2)a	36.4 (8.1)ab	81.9 (4.2)a
Stable fly	69.1 (5.0)a	43.8 (3.1)b	28.3 (6.4)ab	64.5 (3.1)b
S. bullata	36.9 (4.8)b	17.7 (3.1)c	50.6 (9.9)a	43.3 (6.2)c
H. aenescens	76.0 (3.2)a	56.3 (2.8)a	17.1 (5.0)b	74.8 (3.2)a
ANOVA *F*	13.41[a]	26.86[a]	3.01[b]	16.2[a]
Kazakhstan strain				
Horn fly	70.1 (4.0)b	47.5 (3.2)bc	33.8 (7.5)a	67.3 (1.7)ab
House fly	76.9 (3.3)ab	57.1 (3.3)ab	32.1 (5.7)a	73.8 (2.6)a
Stable fly	78.4 (6.4)ab	44.0 (3.7)c	32.8 (8.2)a	57.8 (3.4)bc
S. bullata	47.5 (6.3)c	25.8 (4.0)d	36.8 (6.8)a	55.1 (4.3)c
H. aenescens	89.3 (1.6)a	67.7 (1.5)a	44.7 (6.9)a	75.9 (1.2)a
ANOVA *F*	11.00[a]	23.0[a]	0.53[c]	10.50[a]
Florida strain				
Horn fly	63.2 (2.8)a	46.0 (3.1)a	43.8 (5.1)a	71.5 (1.9)a
House fly	68.1 (4.4)a	55.0 (4.2)a	47.4 (6.3)a	80.2 (2.8)a
Stable fly	65.7 (3.3)a	49.0 (3.1)a	31.9 (7.2)a	74.5 (3.0)a
S. bullata	67.1 (3.7)a	34.1 (3.3)b	51.6 (4.5)a	49.6 (2.9)b
H. aenescens	72.9 (3.7)a	48.9 (2.9)a	16.0 (3.9)b	67.8 (3.1)ab
ANOVA *F*	0.99[c]	4.71[a]	5.70[a]	14.99[a]

$n = 15$ sets of five females (five separate tests of three sets each) with 100 host pupae of each species for a 48-h exposure. Host use is the percent of killed hosts from which adult parasitoids emerged. Means within columns of the same strain followed by the same letter are not significantly different at $P = 0.05$ (Tukey's HSD). ANOVA df = 4,70.
[a] $P \leq 0.01$; [b] $P \leq 0.05$; [c] $P > 0.05$.

Table 5. Mean (SE) no. host attacks and progeny produced by three strains of *S. endius* using five species of hosts

Host	No. hosts killed	No. progeny produced	Percent females	Host use
Russian strain				
Horn fly	65.6 (3.3)b	47.6 (3.1)b	65.4 (5.4)a	72.9 (3.1)a
House fly	81.6 (3.0)a	57.8 (2.4)a	60.5 (2.1)a	70.8 (1.6)a
Stable fly	73.9 (4.1)ab	48.2 (2.7)b	62.2 (3.2)a	66.3 (3.1)ab
S. bullata	44.0 (4.3)c	23.4 (2.4)c	67.5 (4.1)a	57.0 (4.8)b
H. aenescens	82.1 (2.7)a	60.9 (2.1)a	59.9 (2.7)a	74.7 (2.2)a
ANOVA *F*	18.94[a]	31.00[a]	0.72[c]	4.92[a]
Kazakhstan strain				
Horn fly	70.3 (3.9)b	54.3 (4.6)b	61.6 (2.8)a	73.6 (4.3)a
House fly	82.6 (5.3)ab	65.3 (4.4)ab	64.4 (2.9)a	78.8 (2.2)a
Stable fly	88.2 (2.7)a	60.4 (2.4)ab	65.5 (2.8)a	69.0 (2.7)a
S. bullata	41.3 (6.6)c	23.9 (4.6)c	64.4 (2.9)a	53.4 (4.5)b
H. aenescens	94.5 (1.5)a	73.3 (2.1)a	62.0 (1.7)a	77.6 (2.0)a
ANOVA *F*	22.14[a]	23.02[a]	0.35[c]	8.56[a]
Florida strain				
Horn fly	67.9 (2.8)b	48.5 (3.3)b	61.0 (3.4)a	71.5 (3.9)a
House fly	85.1 (2.1)ab	62.3 (2.2)ab	62.1 (3.6)a	73.4 (2.2)a
Stable fly	81.9 (3.6)ab	54.5 (2.2)b	61.9 (1.9)a	67.4 (2.5)a
S. bullata	50.7 (6.8)c	24.5 (3.6)c	71.7 (4.0)a	48.0 (4.0)b
H. aenescens	91.3 (1.3)a	67.5 (2.2)a	64.3 (2.3)a	74.1 (2.4)a
ANOVA *F*	17.86[a]	30.78[a]	1.82[c]	10.22[a]

$n = 15$ sets of five females (five separate tests of three sets each) with 100 host pupae of each species for a 48-h exposure. Host use is the percent of killed hosts from which adult parasitoids emerged. Means within columns of the same strain followed by the same letter are not significantly different at $P = 0.05$ (Tukey's HSD). ANOVA df = 4,70.

[a] $P \leq 0.01$; [b] $P \leq 0.05$; [c] $P > 0.05$.

Spalangia gemina attacked significantly more *H. aenescens* (79.7 pupae killed), house fly (77.4) and stable fly (71.9) than the other two species (51.3 and 42.3 pupae killed for horn fly and *S. bullata*, respectively; Table 7). Progeny production from *S. bullata* (23.2 progeny produced) was significantly lower than from the other host species (40.6–57.3). Host species had no significant effect on sex ratios of *S. gemina;* however, host use was highest with horn fly and house fly hosts (78.6 and 76.7% successful parasitism, respectively) followed by stable fly and *H. aenescens* (65.8 and 64.9%, respectively). Host use was significantly lower in tests with *S. bullata* (51.7%) than with the other four host species.

Dirhinus himalayanus attacked and produced progeny from significantly fewer horn flies (15.7 hosts killed, 5.9 progeny produced) than in tests with the other host species (Table 7). Host attacks were highest on *H. aenescens* and *S. bullata* (86.6 and 76.3 pupae killed, respectively), followed by stable fly (60.1) and house fly (46.3). Progeny production was significantly higher on *H. aenescens* (57.1 progeny produced) than on house fly (29.2), stable fly (33.0), or *S. bullata* (36.4). Host use was significantly lower in tests with horn fly (30.0% successful parasitism) than in tests with the other four host species (49.9–65.7).

Discussion

Recent years have witnessed renewed interest in filth fly parasitoids because of the combined effects of insecticide resistance in target fly populations, loss of

Table 6. Mean (SE) no. host attacks and progeny produced by two strains of *S. nigroaenea* using five species of hosts

Host	No. hosts killed	No. progeny produced	Percent females	Host use
Russian strain				
Horn fly	36.0 (3.7)b	20.7 (2.7)b	48.6 (5.0)a	56.8 (4.9)a
House fly	66.4 (5.3)a	38.9 (3.7)a	55.9 (2.2)a	59.1 (2.6)a
Stable fly	46.2 (3.9)b	21.0 (2.8)b	55.3 (3.9)a	46.3 (3.2)ab
S. bullata	15.1 (3.3)c	3.5 (1.1)c	41.3 (9.1)a	17.2 (3.8)c
H. aenescens	61.2 (7.0)a	26.5 (3.2)b	49.9 (5.3)a	40.8 (3.7)b
ANOVA *F*	17.68[a]	18.33[a]	1.21[c]	18.15[a]
Kazakhstan strain				
Horn fly	31.1 (3.3)b	15.9 (2.4)b	61.8 (4.5)a	46.6 (4.4)a
House fly	61.7 (5.1)a	35.5 (4.8)a	63.0 (4.5)a	55.2 (5.3)a
Stable fly	47.9 (4.1)a	22.7 (2.6)b	66.3 (3.4)a	43.8 (3.2)a
S. bullata	10.8 (3.6)c	1.9 (1.0)c	52.8 (8.3)a	8.3 (4.2)b
H. aenescens	61.7 (2.6)a	26.6 (2.1)ab	51.9 (4.8)a	42.4 (1.9)a
ANOVA *F*	27.63[a]	16.99[a]	1.8[c]	15.56[a]

$n = 15$ sets of five females (five separate tests of three sets each) with 100 host pupae of each species for a 48-h exposure. Host use is the percent of killed hosts from which adult parasitoids emerged. Means within columns of the same strain followed by the same letter are not significantly different at $P = 0.05$ (Tukey's HSD). ANOVA df = 4,70.

[a] $P \leq 0.01$; [b] $P \leq 0.05$; [c] $P > 0.05$.

Table 7. Mean (SE) no. host attacks and progeny produced by *S. gemina* and *D. himalayanus* using five species of hosts

Host	No. hosts killed	No. progeny produced	Percent females	Host use
S. gemina				
Horn fly	51.3 (3.4)b	40.6 (3.2)b	58.6 (4.1)a	78.6 (2.4)a
House fly	77.4 (1.3)a	57.3 (2.5)a	46.3 (8.6)a	76.7 (1.9)a
Stable fly	71.9 (5.0)a	46.9 (3.4)ab	56.4 (2.1)a	65.8 (2.6)b
S. bullata	42.3 (6.6)b	23.2 (4.3)c	64.7 (4.2)a	51.7 (3.3)c
H. aenescens	79.7 (3.2)a	52.1 (3.4)ab	48.2 (5.8)a	64.9 (2.7)b
ANOVA *F*	15.11[a]	14.90[a]	1.96[c]	16.77[a]
D. himalayanus				
Horn fly	15.7 (2.9)d	5.9 (2.2)c		30.0 (7.5)b
House fly	46.3 (5.1)c	29.2 (4.4)b		60.9 (4.5)a
Stable fly	60.1 (6.2)bc	33.0 (4.7)b		52.4 (5.0)a
S. bullata	76.3 (4.3)ab	36.4 (2.0)b		49.9 (4.0)a
H. aenescens	86.6 (3.0)a	57.1 (2.8)a		65.7 (1.7)a
ANOVA *F*	38.5[a]	28.7[a]		7.8[a]

$n = 15$ sets of five females (five separate tests of three sets each) with 100 host pupae of each species for a 48-h exposure. Host use is the percent of killed hosts from which adult parasitoids emerged. Means within columns of the same strain followed by the same letter are not significantly different at $P = 0.05$ (Tukey's HSD). ANOVA df = 4,70.

[a] $P \leq 0.01$; [b] $P \leq 0.05$; [c] $P > 0.05$.

registrations for pesticides labeled for fly control, and environmental concerns about pesticide use near food animals. In particular, there have been numerous surveys of native parasitoids outside the United States to identify dominant or promising local parasitoids for fly biological control. Such surveys of house fly and stable fly parasitoids have been conducted recently in Denmark (Skovgard and Jespersen 1999, 2000, Skovgard and Steenberg 2002), Hungary (Hogsette et al. 2001), Israel (Havron and Margalit 1991), South Korea (Rueda et al. 1997), Malaysia (Sulaiman et al. 1990), India (Srinivasan and Balakrishnan 1989), China (Guo et al. 1997), Brazil (Ferreira de Almeida and Pires do Prado 1999, Monteiro and Pires do Prado 2000), Canada (Floate et al. 1999, McKay and Galloway 1999), and elsewhere. The guild of parasitoids found in different geographic regions is remarkably similar and generally includes *Muscidifurax raptor*, *Spalangia endius*, *S. nigroaenea*, and *S. cameroni.* In addition, *S. gemina* and *Dirhinus himalayanus* are commonly found in tropical/subtropical habitats.

Horn fly parasitoids have received comparatively little attention. *M. raptor*, *S. endius*, *S. cameroni*, *S. nigroaenea*, *S. drosophilae*, and *Trichopria* spp. commonly parasitize horn fly pupae in the United States and Brazil (Figg et al. 1983, Roth 1989, McKenzie and Richerson 1993, Mendes and Linhares 1999, Sereno 2000, Marchiori et al. 2000, 2002).

Little is known about intraspecific variation among parasitoids from different regions, and one of our goals was to examine the relative performance of different geographic strains of common species that were available to us. A second goal was to use standard testing methods to evaluate the effects of host species on attack rate and progeny production of six of the most common parasitoids. In addition to the three pest fly species above, we included two other flies for comparison in these tests, *Hydrotaea aenescens* and *Sarcophaga bullata. H. aenescens* was included because this fly occurs sympatrically with house fly in poultry manure and is sometimes viewed as a beneficial insect because of the habit of its larvae to attack those of house fly (Hogsette and Jacobs 1999). *S. bullata* was included because of its large size (>20 times larger than horn fly), the common occurrence of blow flies and flesh flies around animal production units, and the fact that this species is known to support development of related pteromalids (Rivers 1996).

Sarcophaga bullata was a relatively poor host for *M. raptor* and the four *Spalangia* spp. tested. Attack rates were generally low on this host, as was progeny production and the proportion of successfully parasitized killed pupae. This was most pronounced in tests with *S. nigroaenea*, which produced almost no progeny on *S. bullata.* The reason for low rates of successful parasitism in this host is uncertain, because this species has been used successfully in laboratory tests with *Nasonia vitripennis* (Walker) and *M. zaraptor* Kogan and Legner (Ohgushi 1959, Rivers 1996, Rivers et al. 1998). *M. zaraptor* females spend more time engaged in envenomizing behavior on *S. bullata* than on house fly hosts (Rivers 1996), perhaps reflecting the greater difficulty of drilling through the thick puparium of *S. bullata* and delivering a sufficient quantity of venom to incapacitate such a large host. In contrast, we observed that the large-bodied *D. himalayanus* performed as well on *S. bullata* as on most of the other host species.

Attack rates and progeny production by the parasitoids were generally similar in tests involving the three muscids with similar body sizes (house fly, stable fly, and *H. aenescens*), although progeny production by *S. nigroaenea* was somewhat lower on stable fly hosts than the other species. Responses with horn fly hosts were more variable. *D. himalayanus* produced very few progeny on horn fly pupae. This is not surprising given the relative sizes of host and parasitoid in this instance (*D. himalayanus* adults are about the same size as a horn fly pupa). *S. endius*, *S. nigroaenea*, and *S. gemina* generally attacked fewer pupae and produced fewer progeny on horn fly than on other muscid fly hosts. Results with *S. cameroni* and *M. raptor* were mixed and confounded by small strain differences, but overall, these parasitoids attacked and produced prog-

eny from horn fly hosts at rates similar to tests with the other muscids.

Overall strain differences in this study were low and did not reveal any biotypes with clearly superior properties among those species for which we had both native and exotic strains (*M. raptor*, *S. cameroni*, and *S. endius*). These species are cosmopolitan (Boucek 1963, Kogan and Legner 1970), and the low genetic variation among parasitoids caused by haplo-diploidy makes the discovery of superior biotypes a difficult process. Further research may lead to the discovery of novel species with unique life history characteristics or that target flies at points in the life cycle that represent relatively empty niches.

Our results with horn fly hosts support field survey data suggesting that several of these species may be promising biological control agents for this important pest. These laboratory tests were intended to examine parasitoid performance in standardized single-host testing bioassays to examine host–parasitoid interactions under conditions that optimize chances for successful outcomes. Foraging behavior and parasitism under field conditions is a more complex matter requiring parasitoids to make decisions regarding host habitat selection, host preferences within habitats, and the amount of time to spend searching in patches of varying host densities. Our results thus represent a starting point and are not intended to forecast parasitism patterns in the field. For example, although our bioassays indicated that *S. nigroaenea* was a relatively poor horn fly parasitoid, ecological factors may work in favor of this species in the field. *S. nigroaenea* is commonly found in exposed outdoor settings such as feedlots (Jones and Weinzierl 1997, Rueda et al. 1997) and has been reported to be a dominant parasitoid of horn fly in the field (Mendes and Linhares 1999, Sereno 2000, Marchiori et al. 2000). Further research would be required to determine which parasitoid species would be appropriate for a release program and whether the operational challenges of deploying parasitoids in open rangeland can be resolved.

Acknowledgments

The authors thank H. Brown and H. McKeithen for assisting with fly rearing and bioassays.

References Cited

Andress, E. R., and J. B. Campbell. 1994. Inundative releases of pteromalid parasitoids (Hymenoptera: Pteromalidae) for the control of stable flies, *Stomoxys calcitrans* (L.) (Diptera: Muscidae) at confined cattle installations in west central Nebraska. J. Econ. Entomol. 87: 714–722.

Bailey, D. L. 1970. Forced air for separating pupae of house flies from rearing medium. J. Econ. Entomol. 63: 400–405.

Boucek, Z. 1963. A taxonomic study in *Spalangia* Latr. (Hymenoptera: Chalcidoidea). Acta Entomol. Musei Nationalis Pragae. 35: 429–512.

Crespo, D. C., R. E. Lecuona, and J. A. Hogsette. 1998. Biological control: an important component in integrated management of *Musca domestica* (Diptera: Muscidae) in caged-layer poultry houses in Buenos Aires, Argentina. Biol. Control. 13: 16–24.

Crespo, D. C., E. E. Lecuona, and J. A. Hogsette. 2002. Strategies for controlling house fly populations resistant to cyromazine. Neotrop. Entomol. 31: 141–147.

Ferreira de Almeida, M. A., and A. Pires do Prado. 1999. *Aleachara* spp. (Coleoptera: Staphilinidae) and pupal parasitoids (Hymenoptera: Pteromalidae) attacking symbovine fly pupae (Diptera: Muscidae, Sarcophagidae and Otitidae) in Southeastern Brazil. Biol. Control. 14: 77–83.

Figg, D. E., R. D. Hall, and G. D. Thomas. 1983. Insect parasites associated with Diptera developing in bovine dung pats on central Missouri pastures. Environ. Entomol. 12: 961–966.

Floate, K., B. Khan, and G. Gibson. 1999. Hymenopterous parasitoids of filth fly (Diptera: Muscidae) pupae in cattle feedlots. Can. Entomol. 131: 347–362.

Geden, C. J. 1996. Modeling host attacks and progeny production of *Spalangia gemina*, *S. cameroni* and *Muscidifurax raptor* (Hymenoptera: Pteromalidae) at constant and variable temperatures. Biol. Control. 7: 172–178.

Geden, C. J. 1997. Development models of the filth fly parasitoids *Spalangia gemina*, S. cameroni, and *Muscidifurax raptor* (Hymenoptera: Pteromalidae) under constant and variable temperatures. Biol. Control. 9: 185–192.

Geden, C. J. 1999. Host location by house fly parasitoids in poultry manure at different moisture levels and host densities. Environ. Entomol. 28: 755–760.

Geden, C. J. 2002. Effect of habitat depth on host location by five species of parasitoids (Hymenoptera: Pteromalidae, Chalcididae) of house flies (Diptera: Muscidae) in three types of substrates. Environ. Entomol. 31: 411–417.

Geden, C. J., D. C. Steinkraus, R. W. Miller, and D. A. Rutz. 1992a. Suppression of house flies on New York and Maryland dairies using *Muscidifurax raptor* in an integrated management program. Environ. Entomol. 21: 1419–1426.

Geden, C. J., D. A. Rutz, J. G. Scott, and S. J. Long. 1992b. Susceptibility of house flies (Diptera: Muscidae) and five pupal parasitoids (Hymenoptera: Pteromalidae) to abamectin and seven commercial insecticides. J. Econ. Entomol. 85: 435–440.

Geden, C. J., Long, S. J., Rutz, D. A., and Becnel, J. J. 1995. *Nosema* disease of the parasitoid *Muscidifurax raptor* (Hymenoptera: Pteromalidae): prevalence, patterns of transmission, management, and impact. Biol. Control. 5: 607–614.

Guo, Yu-Jie, J. A. Hogsette, G. L. Greene, and C. J. Jones. 1997. Survey report on pupal parasites of filth flies in livestock and poultry facilities in China. Chinese J. Biol. Control. 13: 106–109.

Havron, A., and J. Margalit. 1991. Pupal parasitoids (Hymenoptera: Pteromalidae) of muscoid filth flies in Israel. Med. Vet. Entomol. 5: 267–275.

Hogsette, F. A. 1992. New diets for production of house flies and stable flies (Diptera: Muscidae) in the laboratory. J. Econ. Entomol. 85: 2291–2294.

Hogsette, J. A., and F. Washington. 1995. Quantitative mass production of *Hydrotaea aenescens* (Diptera: Muscidae). J. Econ. Entomol. 88: 1238–1242.

Hogsette, J. A., and R. D. Jacobs. 1999. Failure of *Hydrotaea aenescens*, a larval predator of the house fly, *Musca domestica* L., to establish in wet poultry manure on a commercial farm in Florida, USA. Med. Vet. Entomol. 13: 349–354.

Hogsette, J. A., R. Farkas, and C. Thuroczy. 2001. Hymenopteran pupal parasitoids recovered from house fly and stable fly (Diptera: Muscidae) pupae collected on live-

stock facilities in Southern and Eastern Hungary. Environ. Entomol. 30: 107–111.

Jones, C. J., and R. A. Weinzierl. 1997. Geographical and temporal variation in pteromalid (Hymenoptera: Pteromalidae) parasitism of stable fly and house fly (Diptera: Muscidae) pupae collected from Illinois cattle feedlots. Environ. Entomol. 42: 421–432.

Kaufman, P. E., S. J. Long, D. A. Rutz, and J. K Waldron. 2001. Parasitism rates of *Muscidifurax raptorellus* and *Nasonia vitripennis* (Hymenoptera: Pteromalidae) after individual and paired releases in New York poultry facilities. J. Econ. Entomol. 94: 593–598.

Kogan, M., and E. F. Legner. 1970. A biosystematic revision of the genus *Muscidifurax* (Hymenoptera: Pteromalidae) with descriptions of four new species. Can. Entomol. 102: 1268–1290.

Marchiori, C. H., A. T. Oliveira, and A. X. Linhares. 2000. Species of *Spalangia* (Hymenoptera: Pteromalidae: Spalanginae) as parasitoids of pupae of muscoid dipterous insects in cattle feces in Goias State, Brazil. Arquivo Brasil. Med. Vet. Zool. 52: 357–359.

Marchiori, C. H., E. R. Caldas, and K.G.S. Almeida. 2002. Microhymenopterous parasitoids collected in cattle dung in Itumbiara, Goias. Arquivo Brasil. Med. Vet. Zool. 54: 454–456.

McKay, T., and T. D. Galloway. 1999. Survey and release of parasitoids (Hymenoptera) attacking house and stable flies (Diptera: Muscidae) in dairy operations. Can. Entomol. 131: 743–756.

McKenzie, C. L., and J. J. Richerson. 1993. Parasitoids of the horn fly in rangeland ecosystems of trans-pecos Texas. Southwest. Entomol. 18: 57–59.

Mendes, J., and A. X. Linhares. 1999. Diapause, pupation sites and parasitism of the horn, fly, Haematobia irritans, in southeastern Brazil. Med. Vet. Entomol. 13: 185–190.

Meyer, J.A.B. A. Mullens, T. L. Cyr, and C. Stokes. 1990. Commercial and naturally occurring fly parasitoids (Hymenoptera:Pteromalidae) as biological control agents of stable flies and house flies (Diptera: Muscidae) on California dairies. J. Econ. Entomol. 83: 799–806.

Monteiro, M. R., and A. Pires do Prado. 2000. *Trichopria* sp. (Hymenoptera: Diapriidae) attacking pupae of *Chrysomya putoria* (Wiedemann) (Diptera: Calliphoridae) in a poultry facility. Ann. Soc. Entomol. Bras. 1: 159–167.

Morgan, P. B., and R. S. Patterson. 1990. Efficiency of target formulations of pesticides plus augmentative releases of *Spalangia endius* Walker (Hymenoptera: Pteromalidae) to suppress populations of *Musca domestica* L. (Diptera: Muscidae) at poultry ranches in the southeastern United States, pp. 69–78. *In* D. A. Rutz and R. S. Patterson (eds.), Biocontrol of arthropods affecting livestock and poultry. Westview, Boulder, CO.

Ohgushi, R. 1959. The longevity, egg laying capacity and the number of hosts parasitized by one female of *Mormoniella vitripennis* (walker) (Hymenoptera: Pteromalidae) reared in three species of fly puparia. Insect Ecol. 8: 46–57.

Petersen, J. J., and J. K. Cawthra. 1995. Release of a gregarious *Muscidifurax* species (Hymenoptera: Pteromalidae) for the control of filth flies associated with confined beef cattle. Biol. Control. 5: 279–284.

Petersen, J. J., J. A. Meyer, D. A. Stage, and P. B. Morgan. 1983. Evaluation of sequential releases of *Spalangia endius* (Hymenoptera: Pteromalidae) for control of house flies and stable flies (Diptera: Muscidae) associated with confined livestock in eastern Nebraska. J. Econ. Entomol. 76: 283–286.

Rivers, D. B. 1996. Channges in oviposition behavior of the ectoparasitoids *Nasonia vitripennis* and *Muscidifurax zaraptor* (Hymneoptera: Pteromalidae) when using different species of fly hosts, prior oviposition experience, and allospecific competition. Ann. Entomol. Soc. Am. 89: 466–474.

Rivers, D. B., M. A. Pagnotta, and E. R. Huntington. 1998. Reproductive strategies of 3 species of ectoparasitic wasps are modulated by the response of the fly host *Sarcophaga bullata* (Diptera: Sarcophagidae) to parasitism. Ann. Entomol. Soc. Am. 91: 458–465.

Roth, J. P. 1989. Some effects of methoprene on *Spalangia cameroni*, a parasitoid of horn fly pupae. Southwest. Entomol. 14: 91–96.

Rueda, L. M., P. U. Roh, and J. L. Ryu. 1997. Pupal parasitoids (Hymenoptera: Pteromalidae) of filth flies (Diptera: Muscidae, Calliphoridae) breeding in refuse and poultry and livestock manure in South Korea. J. Med. Entomol. 34: 82–85.

Rutz, D. A., and R. C. Axtell. 1981. House fly (*Musca domestica* L.) control in broiler-breeder poultry houses by pupal parasites (Hymenoptera: Pteromalidae): indiginous parasite species and releases of *Muscidifurax raptor*. Environ. Entomol 10: 343–345.

Rutz, D. A, and R. S. Patterson (eds.). 1990. Biocontrol of arthropods affecting livestock and poultry. Westview, Boulder, CO.

SAS Institute. 1992. SAS users guide: statistics. SAS Institute, Cary, NC.

Sereno, F.T.D.P. 2000. Pupae of the horn fly, *Haematobia irritans*, collected in feces of neolore breed in the Brazilian Pantanal. Pesquisa Agropecuria Brasil. 35: 1685–1688.

Skovgard, H., and J. B. Jespersen. 1999. Activity and relative abundance of hymenopterous parasitoids that attack puparia of *Musca domestica* and *Stomoxys calcitrans* (Diptera: Muscidae) on confined pig and cattle farms in Denmark. Bull. Entomol. Res. 89: 263–269.

Skovgard, H., and J. B. Jespersen. 2000. Seasonal and spatial activity of hymenopterous pupal parasitoids (Pteromalidae and Ichneumonidae) of the house fly (Diptera: Muscidae) on Danish pig and cattle farms. Environ. Entomol. 29: 630–637.

Skovgard, H., and T. Steenberg. 2002. Activity of pupal parasitoids of the stable fly *Stomoxys calcitrans* and prevalence of entomopathogenic fungi in the stable fly and the house fly *Musca domestica* in Denmark. Biol. Control. 47: 45–60.

Skovgard, H., and G. Nachman. 2004. Biological control of house flies *Musca domestica* and stable flies *Stomoxys calcitrans* (Diptera: Muscidae) by means of inundative releases of *Spalangia cameroni* (Hymenoptera: Pteromalidae). Bull. Entomol. Res. 94: 555–567.

Srinivasan, R., and N. Balakrishnan. 1989. Preliminary note on the parasitoids of *Musca domestica* (Diptera: Muscidae) in Pondicherry. Entomon. 14: 349–352.

Sulaiman, S., B. Omar, S., Omar, J. Jeffery, I. Ghauth, and V. Busparani. 1990. Survey of microhymenoptera (Hymenoptera: Chalcidoidea) parasitizing filth flies (Diptera: Muscidae, Calliphoridae) breeding in refuse and poultry farms in Peninsular Malaysia. J. Med. Entomol. 27: 851–855.

Weinzierl, R. A., and C. J. Jones. 1998. Releases of *Spalangia nigroaenea* and *Muscidifurax zaraptor* (Hymenoptera: Pteromalidae) increase rates of parasitism and total mortality of stable fly and house fly (Diptera: Muscidae) pupae in Illinois cattle feedlots. J. Econ. Entomol. 91: 1114–1121.

Received for publication 19 January 2005; accepted 8 November 2005.